THE PHYSIOLOGICAL DIFFERENCES BETWEEN ARTICULATE BRACHIOPODS AND FILTER-FEEDING BIVALVES AS A FACTOR IN THE EVOLUTION OF MARINE LEVEL-BOTTOM COMMUNITIES

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ABSTRACT. Relevant physiological differences are discussed to determine their potential influence on the change in dominance within marine level-bottom communities from articulate brachiopods in the Palaeozoic to filter-feeding bivalves in the Mesozoic and Cenozoic. It is shown that (1) the two groups of animals have overlapped greatly in requirements for food and space during the Phanerozoic, (2) the bivalves have considerably more energy per unit biomass to spend on the production of offspring, (3) filter-feeding bivalves are potentially able to exploit a larger number of habits and to cope more effectively with most environmental factors than are the articulates, and (4) that these bivalves have considerably greater abilities to colonize and to expand their distribution than have the articulates.

Empirical evidence is cited for the importance of competition in Recent marine level-bottom communities in general, and amongst Recent filter-feeding bivalves in these communities in particular. Although competition may occur only occasionally, it seems to be important in shaping long-term structures of level-bottom communities. Competition on the level bottom appears to have been considerably intensified and its effects greatly enhanced at certain times during the Phanerozoic. It is suggested that partitioning of space contributed greatly to the ability of articulate brachiopods and filter-feeding bivalves to share the near-shore region during the Palaeozoic. The fact that filter-feeding bivalves became established close to shore early in the Palaeozoic is attributed to frequent unpredictable physical disruptions of shallow-water communities. A lack of severe physical disturbances offshore probably enabled community structures to be maintained there for considerable periods of geological time; when severe physical changes disrupted these structures at the end of the Permian, bivalves invaded and replaced the articulates as the dominant off-shore invertebrates. The decline of articulate brachiopods and increase in importance of filter-feeding bivalves occurred in a series of steps. It is suggested that because of physiological differences between the two groups, filter-feeding bivalves suffered less than articulates at both the Permian–Triassic and Triassic–Jurassic extinctions; that after each extinction filter-feeding bivalves were able to invade numerous vacant or partially vacant habitats earlier and faster than the articulates; and that competition, particularly from the established bivalves, then prevented articulates from reoccupying many of the habitats that they had previously held. The Cenozoic decline of articulate brachiopods resulted from a loss of their preferred habitats (Ager *in litt.* 1977).

ARTICULATE brachiopods were the dominant fossilizable invertebrates in most level-bottom communities in the Palaeozoic (Bretsky 1969*a*), and filter-feeding bivalves replaced the articulates and dominated these communities in the Mesozoic and Cenozoic (e.g. Rudwick 1970, pp. 182–184). I became interested in the reasons for this change in dominance when working on the problem of brachiopod feeding (Steele-Petrović 1976) and recognized that the two groups have utilized essentially the same food during the Phanerozoic, but that compared with filter-feeding bivalves brachiopods waste considerable energy in almost every physiological aspect of feeding. These facts led me to consider the physiology of other processes, and the ways in which the physiological differences between the two groups could have influenced their fossil record since the Middle Ordovician.

In this paper I compare resource requirements of articulate brachiopods and filter-feeding bivalves, and the ecological advantages of the two groups both in the adult and

larval stages. This comparison shows considerable overlap with bivalves superior, suggesting that competition may have played a role in the changes in dominance. Since competition in level-bottom communities has been disputed frequently (e.g. Johnson 1964; Stanley 1974a; Connell 1975), I discuss evidence on competition in these communities, both in the Recent and in the past. I then consider in some detail the changes in relative abundances of filter-feeding bivalves and articulate brachiopods during the Phanerozoic, and how these changes, and therefore the major structural changes in level-bottom communities, can be explained in terms of the physiological differences that are discussed here.

The brachiopods that I consider are primarily the articulates, as the inarticulates differ from the articulates in many ways, and have played a significant role only in a relatively restricted range of marine communities since the early Ordovician. However, in the first section, on feeding, I commonly discuss brachiopods in general, since all brachiopods feed in essentially the same way (Steele-Petrović 1976).

RESOURCE REQUIREMENTS OF BRACHIOPODS AND FILTER-FEEDING BIVALVES

Space. Brachiopods and filter-feeding bivalves have numerous morphological and physiological similarities: the shapes of their shells are commonly similar; both groups have two valves secreted by a mantle that encloses the soft tissue; all brachiopods and most filter-feeding bivalves are suspension-feeders (for differences between 'filter-feeding' and 'suspension-feeding', see Steele-Petrović 1975); they obtain food from water currents brought into the mantle cavity by beating of lateral cilia located on the feeding organ, and in each case the water passes through the feeding organ, where particles are trapped, and then out as an exhalant current; digestion is very similar in both groups (Steele-Petrović 1976). It is understandable therefore that both groups have had considerable overlap in habits and in habitat requirements during the Phanerozoic. Both groups have had free-living, permanently attached, burrowing, and swimming forms; and both have occupied most marine habitats including intertidal, level-bottom (both shallow and deep water), and reefal.

Food. The available evidence for brachiopods on stomach contents, and on the anatomy, histology, physiology, and biochemistry of their feeding system indicates that their food consists, in varying proportions, of dissolved substances, bacteria, organic colloids, organic detritus, and algae (Steele-Petrović 1976).

Table 1 summarizes information on the food of filter-feeding bivalves. Many authors have claimed that bivalves must assimilate organic detritus (for reviews see Verwey 1952; Jørgensen 1966, pp. 260–263), but the value of such detritus has not been sufficiently examined experimentally; as Jørgensen (1966, pp. 257–258) has indicated, it is very difficult to separate dead organic material from living micro-organisms in the water, and in most experiments that have been performed to show the importance of organic detritus as food, the bacterial content has not been considered, so that positive results could have been due to bacteria rather than to dead organic matter. However, as in the case of brachiopods, there are several lines of indirect evidence that strongly suggest that organic detritus can be utilized by filter-feeding bivalves. First, the dominant enzymes of intracellular and extracellular digestion in bivalves are

TABLE 1. Direct and indirect evidence of foods of filter-feeding bivalves.

Food	References	Comments
Dissolved organic matter	Efford and Tsumura 1973; Khailov *et al.* 1973; Bamford and Gingles 1974; Bamford and McCrea 1975	Uptake may be through body surface. For same reasons as with brachiopods (Steele-Petrović 1976), probably not important source of food
Bacteria	Zobell and Feltham 1938; Newell 1965; Jørgensen 1966, p. 259; Fenchel 1971; Bernard 1974; Hylleberg and Gallucci 1975	
Colloids	Verwey 1952	Evidence of removal from water. May obtain from surface of clay particles as McCammon (1969) suggested for brachiopods
Organic detritus	This paper	See text
Algae	Yonge 1926; Ballantine and Morton 1956; Dean 1958; Allen 1962; Goreau *et al.* 1970; Fenchel 1971; Mathers 1972; Hylleberg and Gallucci 1975	
Minute animals	Nelson 1933; Mansour 1946; Hylleberg and Gallucci 1975	Appears to be relatively unimportant in most cases

carbohydrates (Sova *et al.* 1970; Kristensen 1972*a*; Wojtowicz 1972; Mathers 1973); and organic detritus is relatively high in carbohydrates and low in proteins and lipids (Agatova and Bogdanov 1972), while living material is relatively high in proteins and low in carbohydrates and lipids (Parsons *et al.* 1961; Agatova and Bogdanov 1972). Secondly, methylchitinase in the absence of chitinase, and methylcellulase in the absence of cellulase are usually found in bivalve guts; but methylchitin and methylcellulose only occur as products of the breakdown of chitin and cellulose, and there is usually evidence to indicate that bivalve guts lack large quantities of bacteria capable of hydrolysing chitin and cellulose (Kristensen 1972*a*). These facts suggest that chitin and cellulose are hydrolysed by bacteria in detritus and that the broken-down detritus is subsequently ingested, and at least part of it digested by filter-feeding bivalves. Although suspension-feeders in general may ingest large numbers of larvae (Woodin 1976), such larvae are probably not assimilated by most invertebrates (e.g. Jørgensen 1966, p. 149). The apparent absence of extracellular proteases in brachiopods (Steele-Petrović 1976) suggests an inability, by comparison with that of filter-feeding bivalves, to assimilate minute animals. However, this form of food appears in general to be relatively unimportant for these bivalves. In all other respects the food of the two groups is essentially the same, and I see no reason to suggest that this has not always been the case. Undoubtedly for both groups, as noted by Cowen (1971) for brachiopods, the food of any particular individual depends on habitat, latitude, depth, and season.

Discussion. Since articulate brachiopods and filter-feeding bivalves have utilized essentially the same resources during the Phanerozoic, competition may have played a significant role in the evolution of the two groups.

COMPARATIVE ECOLOGICAL ADVANTAGES OF THE ADULTS OF ARTICULATE BRACHIOPODS AND FILTER-FEEDING BIVALVES

Feeding

When determining whether one group has had a competitive advantage over the other, one factor to consider is the energy intake and the way in which this energy is utilized. In evaluating potential competitive advantages one needs to consider the following three energy factors, each of which is referred to unit biomass and unit time:

1. *Gross energy gain* defined as energy obtained from ingested food. This quantity is a measure of feeding effectiveness, i.e. success in obtaining energy by feeding.

2. *Net energy gain* defined as gross energy gain minus energy expended in feeding. This quantity is a measure of the advantages gained from feeding.

3. *Excess energy gain* defined as net energy gain minus basal metabolic energy (the amount of energy needed to maintain an animal in a state of rest), or gross energy gain minus unavoidable energy costs. The group that obtains greatest excess energy gain per unit biomass and unit time must have a feeding advantage. The excess energy can be channelled into body reserves, fast growth, physiological processes requiring a high expenditure of energy (e.g. stronger feeding, burrowing, swimming), and most significantly into the production of large numbers of offspring. Accordingly, excess energy gain is the measure of competitive ability in feeding.

Feeding efficiency, defined as net energy gain over gross energy gain, is not as important a factor in competitive ability as is net energy gain. In fact, net energy gain is frequently increased at the expense of efficiency. A comparison can be drawn with selling cars, where success depends on maximizing total net profit rather than percentage profit.

Although no data are available on energy intake and utilization, similar steps in the feeding processes of the two groups can be compared, and a qualitative estimate of the relative energy gains at each stage can be made. Providing one group has a feeding advantage at all stages, one can ascertain which animal has the greater total net energy gain. The animal with greater excess energy gain can then be determined, and accordingly the one with competitive superiority, provided that the basal metabolic needs of the two groups are comparable or favour the group with greater net energy gain.

Pumping. The bivalve gill and brachiopod lophophore both act as pumps, and are fundamentally the same morphologically and physiologically in that both are composed of filaments with lateral cilia which beat to produce an inhalant current, and with frontal cilia which transport the trapped material to a groove leading to the mouth (see Rudwick 1970, pp. 117 *et seq.* and Steele-Petrović 1975, 1976, for discussions of lophophore; and Atkins 1936*a*, *b*, *c*, for discussions of gills). Gill filaments are strongly attached, laterally to each other, and distally to the mantle or foot; these attachments are formed either by ciliary junctions or organic fusion. In contrast, lophophoral filaments are never attached to each other, nor are their distal ends attached to any anatomical structure and energy must be expended holding them in place against the mantle surface or body wall, in order to separate inhalant and exhalant chambers (Rudwick 1970, p. 118). Therefore, a bivalve gill can produce a greater pressure difference and hence greater current velocity (Rudwick 1970, pp. 118–120), and can have a greater pumping capacity, than can a brachiopod lophophore with similar cumulative filamental length and similar energy consumption. Accordingly, where

trapping organs are of comparable size, the net energy gained in pumping is potentially greater for filter-feeding bivalves than for articulate brachiopods. In addition, the gill is a more compact structure than the lophophore, because of folding and fusion of the gill sheets back to back, and in some cases plication. This structural modification enables a gill that is considerably shorter than a lophophore to have a comparable pumping capacity.

Trapping of particles. Because of open spaces between the filaments of the lophophore, much of the material suspended in the feeding current of brachiopods is carried between the filaments and into the exhalant chamber (Rudwick 1962*b*; Steele-Petrović 1975). Only those particles are trapped that make contact with the frontal surfaces of the filaments (Rudwick 1962*b*; Bullivant 1968) or with their short lateral cilia (Strathmann 1973). In comparison, latero-frontal cirri on adjacent filaments of the gill of filter-feeding bivalves intermesh across the interfilamentary spaces (Dral 1967; Moore 1971; Owen 1974; Owen and McCrae 1976) and trap all particles in the inhalant current that are larger than the size of the mesh; mesh size in *Mytilus edulis* is 0·6 μm by either 2·4 μm or 4·8 μm, the latter depending on the relative positions of adjacent cirri (Owen 1974). Although energy is consumed by the latero-frontal cirri of bivalves, the amount must be small compared with that which is effectively wasted by the inability of articulates to trap much of the incoming material. Therefore, where pumping organs are of comparable size, the net energy gained at the trapping stage is considerably greater for filter-feeding bivalves than for articulate brachiopods.

Transporting particles to the mouth. Particles that have been accepted as potential food by filter-feeding bivalves are bound in mucus on the frontal surfaces of the filaments (Atkins 1936*a*; Jørgensen 1966, p. 83). In contrast, brachiopods appear to locally reverse the beat of the lateral cilia to prevent particles from escaping while being carried along the frontal cilia (Strathmann 1973), and trapped particles are bound in mucus only after reaching the food groove (e.g. Steele-Petrović 1976). The brachiopod reversal of ciliary beat must consume very much more energy than the bivalve production of mucus, and since reversal decreases the pumping capacity, it effectively wastes considerable energy; in addition, this reversal in brachiopods is unlikely to prevent the escape of motile protistans (cf. Bullivant 1968), or to be as successful as the mucus of filter-feeding bivalves in retaining non-swimming forms. Therefore, when trapping organs of comparable sizes are considered, the net energy gain with respect to the ability to retain trapped particles is considerably greater for filter-feeding bivalves than for articulate brachiopods.

The brachiopod lophophore lacks a sorting mechanism (e.g. Steele-Petrović 1975, 1976) and handles all particles indiscriminately, regardless of potential food value. In contrast, both the gills (e.g. Atkins 1936*a, b, c*) and labial palps (e.g. Yonge 1926; Purchon 1955; Jørgensen 1966, pp. 77–82; Hughes 1975) of filter-feeding bivalves effectively, although imperfectly (Atkins 1936*b*; Hughes 1975), sort the trapped material according to specific gravity (e.g. Atkins 1936*a*), size (e.g. Verwey 1952; Hughes 1975; Hylleberg and Gallucci 1975), and possibly to some extent according to food value (Hughes 1975); the denser and larger particles and particle masses are rejected as pseudofaeces (Atkins 1936*a*; Verwey 1952; Jørgensen 1966, pp. 75–81; Hughes 1975; Hylleberg and Gallucci 1975), and small low density particles, which are

likely to have a greater food value, and can be more readily processed for intracellular digestion (Jørgensen 1966, p. 85), eventually reach the mouth. When suspended material is scarce, sorting by the gills (e.g. Atkins 1936*a*, *b*) and labial palps (e.g. Ansell 1961; cf. Jørgensen 1966, p. 79) greatly decreases and probably frequently ceases. However, Atkins (1936*c*) found that when small quantities of fine carborundum were experimentally dropped on to a gill, only some of the particles were accepted and others were rejected as pseudofaeces. The fact that sorting may occur when only small amounts of material touch the gill suggests that this process is not just a 'costly' method of getting rid of excess trapped particles, but rather that it is advantageous even when potential food and therefore potential energy are scarce. Accordingly, it can be concluded that sorting must consume less energy than it ultimately saves.

Digestion. Morphological and histological evidence indicates that assimilation of food by the digestive diverticula is the same in brachiopods and filter-feeding bivalves (Steele-Petrović 1976); therefore, in order to compare the relative advantages of the methods of digestion in the two groups, it is necessary to consider only those processes that precede assimilation. Although the digestive tracts of the two kinds of animals differ in many ways, the effectiveness and energetics of parallel as well as similar processes can be compared (see Owen 1953, 1955 and Reid 1965, for discussions of digestion in filter-feeding bivalves; and Steele-Petrović 1976, for discussion of brachiopods).

Ingested particles are released from their binding mucus in filter-feeding bivalves by the combined action of stomach pH (Yonge 1935) and rotation of the crystalline style against the gastric shield (Reid 1965); in brachiopods this release must be due to pH alone (Steele-Petrović 1976), and must be a slower and less 'costly' process than in bivalves. However, rotation of the crystalline style in filter-feeding bivalves (Morton 1952; Reid 1965; Kristensen 1972*b*) has a counterpart in rotation of the pyloric protostyle in brachiopods (e.g. see Steele-Petrović 1976), and the energy consumed in these processes is probably similar in both groups of animals.

Since different regions in the stomach of filter-feeding bivalves have different functions (Reid 1965), several steps of the digestive process can occur simultaneously: i.e. sorting of ingested material in the stomach, rejection of dense particles into the intestinal groove (e.g. Reid 1965), and transport of very small particles to the digestive diverticula by the beating of cilia in the diverticular ducts (Owen 1955) all occur at the same time. Therefore, although filter-feeding bivalves do not feed continuously (Morton 1973), within each feeding cycle food is processed in a continuous-flow system where the regime can be adjusted according to the circumstances, and handling of particles of low nutritional value is minimized. In contrast, the digestive tract of brachiopods is morphologically simpler and comparatively undifferentiated, so that no sorting takes place, only one phase of digestion occurs at a time, and ingested particles are handled in batches (e.g. Steele-Petrović 1976). Accordingly, ingestion must cease, and then muscular contractions of the digestive diverticula force ingested particles (regardless of size or potential food value) back and forth between the stomach and digestive diverticula (Steele-Petrović 1976); and the fraction of usable particles in each batch of the handled material must decrease with time. Therefore, under most conditions the digestive system of a feeding bivalve can process

considerably more food in a given time compared with that of a feeding brachiopod of comparable size. The comparative effect of cyclical feeding (Morton 1973) is unknown for there are no data on possible cyclicity in brachiopods (Steele-Petrović 1976). Since neither the digestive cells of brachiopods nor those of filter-feeding bivalves can phagocytose particles that are more than a few microns in diameter (Owen 1955; Steele-Petrović 1976), the bivalve method of transporting only very small particles into the digestive gland, must bring a comparatively larger percentage of potentially usable particles into contact with the digestive cells. The apparent absence of extracellular proteases and lipases in brachiopods (Steele-Petrović 1976) and their presence, although in small concentrations, in filter-feeding bivalves (Mansour-Bek 1945; George 1952; Reid 1966, 1968; Reid and Dunnill 1969; Reid and Rauchert 1970, 1972; Vaskovsky and Suppes 1972) is another indication of the greater effectiveness of the digestive system in these bivalves.

Digestion in filter-feeding bivalves is not only considerably more effective than in articulate brachiopods, but the net energy gained at this stage must also be very much greater in bivalves for the following reasons. In most cases cilia perform a function far more efficiently than can any conceivable muscular mechanism (Prosser and Brown 1961, p. 476); therefore, the ciliary movement of only very small particles to the digestive cells of filter-feeding bivalves must consume just a small fraction of the energy used by brachiopods in the muscular pumping of large quantities of material back and forth between the stomach and digestive diverticula. As with sorting prior to ingestion, it can be argued that sorting in the stomach of these bivalves consumes less energy than it ultimately saves; in fact, considerable amounts of energy must be expended by brachiopods in processing large quantities of ingested material that cannot be digested; whereas the bivalves get rid of much of the unwanted matter by spending comparatively less energy in sorting, both before and after ingestion. In addition, it is hard to imagine that the production of extracellular proteases and lipases is a net energy drain on these bivalves.

Excess energy gain. The above discussion shows that although both filter-feeding bivalves and articulate brachiopods expend considerable amounts of energy in feeding, the energy is in general profitably used by bivalves, whereas much of it is effectively wasted by brachiopods. As a result, filter-feeding bivalves have a considerably greater net energy gain in feeding. It follows that the basic metabolic energy requirements per unit biomass and unit time would have to be much greater for the bivalves than for the articulates in order for the excess energy gain per unit biomass and unit time to be similar in the two groups.

The scanty evidence available suggests that the normal rate of consumption of energy per unit biomass is greater in filter-feeding bivalves than in articulate brachiopods (Hammen 1977); this is a predictable situation, considering the fact that bivalves have more 'costly' methods of reproduction (discussed below) and are generally more active than the articulates. There are no comparative data on basal metabolic rates per unit biomass. However, much of the energy consumed in a resting state must be for oxygen consumption; oxygen is obtained from the inhalant water current which is produced in the same manner by both groups (see above), both types of animals are relatively simple, and many organs and tissues in the two groups are

similar (Steele-Petrović 1976) and probably have comparable oxygen requirements. Therefore, it can be argued that as a first approximation the basic metabolic energy requirements per unit biomass and unit time should not differ greatly in the two groups.

These arguments indicate that the excess energy gain per unit biomass and unit time should be considerably greater for filter-feeding bivalves than for articulate brachiopods. Therefore, in a competitive situation the bivalves should have an advantage over the articulates.

Coping with different environmental factors

Another factor to consider when determining if either filter-feeding bivalves or articulate brachiopods have a potential competitive advantage over the other is their relative abilities to cope with different environmental factors. If one group exploits more effectively a large number of environments, one would expect that group to have a competitive advantage in many situations. If the same group of animals is superior in both feeding and in coping with different environmental factors, that group should be considerably superior to the other in most competitive circumstances.

Morphological plasticity and exploitation of different habits. Articulates have adapted to different conditions only by changes in shape of the shell, size and form of the pedicle, and configuration of the lophophore. The morphology of their 'soft parts' and their physiological processes have probably remained the same, in essential features, throughout the Phanerozoic (Steele-Petrović 1976). Although some articulates have attached to soft organic materials such as sponges, tunicates, algae etc. (Rudwick 1961, 1965, 1970, p. 77; Ager 1967a; Foster 1974, p. 23) and floating seaweed (Ager 1962), have been cemented (Rudwick 1965, 1970, p. 85; Ager 1967a), have lived free on the bottom (Rudwick 1965, 1970, pp. 87–90; Ager 1967a; Bowen 1968) particularly during the Upper Palaeozoic, or have lived partially buried in mobile sands (Richardson and Watson 1975a, b), these modes of life are not typical, and articulates appear to be best suited for pedical attachment to hard substrates. In contrast, filter-feeding bivalves have a greater potential range of typical adaptations, and they have differed greatly, both in size and shape, and in 'soft-part' morphology and physiological processes. They have developed numerous burrowing, byssally attached, free-living, boring, and cemented forms which have successfully adopted infaunal, semi-infaunal, or epifaunal habits in or on soft and hard bottoms (e.g. Stanley 1968, 1970, 1972). Unlike articulates, some of these bivalves are deposit-feeders (Yonge 1949; Pohlo 1969).

The slight structural differences between the bivalve gill and brachiopod lophophore have contributed to the abilities of filter-feeding bivalves to successfully exploit different habits more fully than articulate brachiopods could. If the shape of an animal does not change with size, surface area of a trapping organ is proportional to (volume)$^{2/3}$ of an animal. Hence there is a maximum length of trapping organ beyond which it is too large to be contained within the mantle of the animal. Since the gill is more compact than the lophophore, and for a given length has a greater pumping capacity, it can support a greater biomass than can a lophophore of comparable length. Therefore, filter-feeding bivalves have the potential for attaining larger sizes than do brachiopods; and the greater excess energy gain of the gill over the lophophore further enhances this potential. The fact that filter-feeding bivalves have the potential

to grow to be larger than brachiopods, and therefore can span a greater size range, has almost certainly contributed to the abilities of these bivalves to successfully exploit different habits and habitats more fully than articulate brachiopods.

In addition, a compact gill leaves room inside the valves for an even larger gill in relation to the biomass, or for other anatomical features such as the foot. The brachiopod lophophore may occupy seven-eighths of the mantle cavity (Reynolds and McCammon 1977) and appears to leave little space for other structures. Since the bivalve foot varies greatly from a muscular burrowing organ to a small reduced structure that produces byssal threads, it has enabled bivalves to assume a number of adaptive roles that cannot be assumed by brachiopods. The greater excess energy gain of filter-feeding bivalves over brachiopods must give these bivalves relatively more energy to expend on such functions as burrowing or swimming, reproduction, and stronger pumping. The development of the eulamellibranch gill with its large pumping capacity contributed to the Mesozoic exploitation of the deep infaunal siphonate habit by filter-feeding bivalves (Stanley 1968). In contrast, a brachiopod lophophore, because of its basic design, is limited to changes in length, and could never be modified to have sufficient pumping capacity for siphons to be functional; as a result, brachiopods have remained epifaunal except for the lingulids, whose valves open at the surface of the sediment during feeding.

The importance of the eulamellibranch gill in deep burrowing forms has generally not been emphasized along with that of mantle fusion (Stanley 1968, 1972). A shallow pallial sinus was present in the Ordovician genus *Lyrodesma* (Newell and LaRocque 1969); it also occurred in several genera of anomalodesmatans up to 100 million years before relatively deep-burrowing forms of that Subclass appeared in the Carboniferous (Runnegar 1974). Therefore, the exploitation of deep infaunal habits should not have been prevented by the absence of mantle fusion and siphons. Another consideration is that deep-burrowing siphonate bivalves require eulamellibranch gills to produce a current with sufficient velocity to overcome the friction of a long siphon. If the classification of *Lyrodesma* as a trigonid is correct, that genus must have had a filibranch gill for one would not expect it to have had a more advanced gill than all Recent representatives of the group. Palaeontological evidence does not permit one to determine whether the early anomalodesmatans already had eulamellibranch gills (Runnegar 1974). Therefore, it is conceivable that it was the lack of a eulamellibranch gill that prevented early Palaeozoic filter-feeding bivalves from becoming deep burrowers.

The above discussion indicates that the basic structure of filter-feeding bivalves lends itself to greater morphological and physiological variability than does that of brachiopods. (Schopf *et al.* (1975) argued that articulates are morphologically more complex than bivalves, but these authors considered only shell morphology.) In the course of the Phanerozoic, the greater inherent potential of filter-feeding bivalves for evolutionary change has enabled them to become more specialized and to exploit a greater number of habits, compared with brachiopods.

Eurytopy versus Stenotopy. Many filter-feeding bivalves are eurytopic as exemplified by the fact that as a group they have successfully exploited the intertidal zone since the Middle Ordovician (my own unpublished information). In contrast, articulate

brachiopods are comparatively stenotopic and only a relatively few species have ever lived intertidally; most of these intertidal forms such as the Ordovician genus *Zygospira* (Walker and Laporte 1970; my own unpublished information from the Ottawa Valley, Canada), Devonian *Howellella* (Walker and Laporte 1970), and the Recent species *Waltonia inconspicua, Tegulorhynchia nigrans*, and *Pumilus antiquatus* (Percival 1944, 1960; Rudwick 1962a, b; Rickwood 1968) occupy(ed) tidal channels or pools; Percival (1944) and Bowen (1968) reported *W. inconspicua* and Thayer (1975, 1977) reported *Terebratalia transversa* from above low tide mark, but such occurrences are not nearly as common for articulate brachiopods as for filter-feeding bivalves. Since the salinity tolerance of articulates is greater than was previously thought, it is uncertain what physiological characteristics prevent(ed) this group from generally living intertidally (Thayer 1974), although an inability to withstand dessication may be a factor (cf. Thayer 1975).

Turbulence. Since the attachment strengths of the pedicle and byssus appear to be comparable (Thayer 1975), both groups of animals are able to tolerate similar energy regimes, providing a firm area of attachment is available. However, shifting sediment frequently occurs in turbulent water, and very few articulates can tolerate this disturbance (but see Richardson and Watson 1975a, b); in contrast, infaunal filter-feeding bivalves, particularly those that can burrow rapidly, are able to readily adjust to shifts in the substrate.

Sedimentation rate. Articulate brachiopods are generally unable to tolerate a high rate of sedimentation (Rudwick 1970, p. 159). On the other hand, many filter-feeding bivalves can move as the position of the sediment-water interface changes.

Turbidity. As mentioned above, brachiopods trap only a fraction of material suspended in the inhalant current, whereas filter-feeding bivalves trap virtually all particles. Therefore, in turbid conditions it would be necessary for most filter-feeding bivalves, but not brachiopods, to spend a great deal of energy sorting and transporting the trapped material, and beyond a certain turbidity the sorting and transport mechanisms would probably become clogged and inoperable.

The few bivalve species that live where the water is turbid are secondarily adapted for handling large amounts of suspended material. For example, in siphonate suspension-feeders, straining tentacles surround the aperture of the inhalant siphon (e.g. Yonge 1949; Ansell 1961; Pohlo 1972; Narchi 1972, 1975) and interdigitate across the opening to keep out suspended material; in at least one family, the Veneracea, the tentacles are particularly well developed only in those species living in turbid environments (Pohlo 1972). Various modifications in the margin of the mantle (Nelson 1938), and different kinds of membranes at the base of the siphons (Dodgson 1928; Yonge 1949; Ansell 1961) are found in many bivalves living in turbid environments. These features enable such bivalves to control the flow of water through the mantle cavity and to direct much of the suspended material away from the gills. Deposit-feeding tellinaceans, which are modified to suck in large amounts of bottom material, lack straining tentacles on the end of the siphon (Pohlo 1972); but a pair of mantle folds at the base of the siphon collects pseudofaeces and prevents them from being washed forward by the inhalant current (Yonge 1949; Pohlo 1972); these deposit-feeders also have smaller gills and larger palps than the suspension-feeders, so that

most of the trapped material is passed to the palps (Atkins 1936b, c), which appear to reject excess mucus-bound material rather than sorting individual particles according to size and weight as they do in other filter-feeding bivalves (Reid and Reid 1969). Therefore, certain filter-feeding bivalves have greatly overcome the basic difficulty that the bivalve gill has in handling large amounts of suspended material; and some of these bivalves may be able to cope with turbid environments as successfully as brachiopods; however, this tolerance for suspended sediment has been achieved only through secondary adaptations.

Food requirements. Compared with filter-feeding bivalves, articulate brachiopods appear to have lower rates of oxygen consumption (Hammen 1977), cannot grow as large (discussed above), and more commonly brood their larvae (see below). A large part of energy output in marine invertebrates goes into producing offspring (Vance 1973), and production of brooded larvae requires considerably less energy than production of planktotrophic larvae (Mileikovsky 1971; Menge 1975). Therefore, these observations indicate that articulate brachiopods should need less food than filter-feeding bivalves.

Indirect evidence of the need for less food by articulates is that they frequently live in deep water (e.g. McCammon 1969, 1973; Foster 1974) where food is relatively scarce (Jørgensen 1966, pp. 273 *et seq.*; Raymont 1971) and where filter-feeding bivalves are often small or rare (e.g. Foster 1974, p. 23). There is even evidence to suggest that the Mesozoic articulate *Pygope* lived in the absence of other suspension-feeders where food was scarce (Ager 1965, 1967b; Vogel 1966). The present occurrence of brachiopods and absence of filter-feeding bivalves in cryptic habitats in reefs (Jackson *et al.* 1971; Logan 1975) may also be related to a shortage of food.

Coping with predation

Stanley (1974b) argued that smaller size, thinner shells, epifaunal habit, and lack of mobility are features of brachiopods that in general make them more susceptible to predation than bivalves. However, the fact that an animal can be more easily killed does not ensure that it is preferentially attacked. In fact R. T. Paine (pers. comm.) has a small amount of evidence suggesting that Recent predators generally take bivalves before brachiopods. This fact is in accordance with the relative scarcity of brachiopods today and their comparatively small biomass. However, brachiopods may have been more susceptible to predation during the Palaeozoic when they were a common part of the benthos and therefore more easily found.

COMPARATIVE ECOLOGICAL ADVANTAGES OF THE LARVAE OF ARTICULATE BRACHIOPODS AND FILTER-FEEDING BIVALVES

Larvae of most articulate brachiopods have a relatively short free-swimming period of usually a few hours or at most a few days (Ager 1967a; Rudwick 1970, p. 155), and in many species the larvae are brooded within the shell of the mother (e.g. Percival 1944, 1960; Atkins 1960; Rickwood 1968; Rudwick 1970, p. 153; Webb *et al.* 1976). On the other hand, most filter-feeding bivalves, particularly those that live in tropical and temperate shelf zones, have planktotrophic larvae (Mileikovsky 1971), although

lecithotrophic larvae appear to be important in bivalves inhabiting high latitudes and great depths (Mileikovsky 1971). This free-swimming larval stage appears to last for up to five weeks in most bivalves (Muus 1973).

A short planktonic larval stage and brooding within the parent favour a clumped distribution of a species; clumping can lead to local extinction in the presence of a minor adversity, or to total extinction at the disappearance of a major habitat. Conversely, a relatively long planktonic period favours a wider distribution of a species, permits quicker recovery of populations that have been locally damaged, and under favourable conditions enables quicker expansion, including colonization of new habitats (Mileikovsky 1971).

Planktotrophic larvae must have functional digestive tracts long before settling; and gill-palp feeding organs of bivalves are usually functioning two or three days after settling has occurred (Bayne 1971). In contrast, new articulate spat have only incomplete rudimentary guts (Percival 1944, 1960; Rickwood 1968), and the lophophore does not begin to develop in *Waltonia inconspicua* until after the gut has opened through the mouth which is not 'for some time' after settling (Percival 1944). Also, bivalves, including bivalves that do not have planktotrophic larval stages, have grown a shell by the time settling has occurred (Cox 1969). Studies by Percival (1944) and Rickwood (1968) indicate that articulates do not begin to grow a shell until after they have settled; Rickwood reported that the shell of *Pumilus antiquatus* did not appear until three or four days after settling and that the spat were particularly susceptible to predation by ciliates and polychaetes before that time. Rickwood's report implies that resistance to predation increases measurably once articulates produce a shell. Therefore, although newly settled spat of bivalves are also exceedingly vulnerable (Muus 1973), their weak shells may be protection from the tiniest predators (e.g. ciliates and very small polychaetes) that effectively attack the newly settled articulate spat of the only species for which evidence of this type is available. Since vulnerability to predation generally decreases with size it is advantageous for an animal to grow as quickly as possible. However, there are insufficient comparative data on the early growth of articulates and filter-feeding bivalves to determine if either group has an advantage at this stage of development.

The comparative ecological advantages of articulate brachiopods and filter-feeding bivalves are summarized in Table 2.

EVIDENCE OF COMPETITION IN RECENT MARINE LEVEL-BOTTOM COMMUNITIES

During the Phanerozoic, filter-feeding bivalves replaced articulate brachiopods as the dominant fossilizable invertebrates in most marine level-bottom communities (see below). I have already shown that these two groups overlapped considerably in requirements for food and space throughout this time, and that in general the bivalves have a potential for gaining more energy in feeding, exploiting a larger number of habits, and coping more effectively with environmental factors than the brachiopods. Such facts raise the possibility that competition between articulate brachiopods and filter-feeding bivalves was a significant factor in the evolution of marine level-bottom communities. However, several authors have recently concluded that competition is

TABLE 2. Summary of comparative ecological advantages of articulate brachiopods and filter-feeding bivalves.

Advantages	Articulate brachiopods	Filter-feeding bivalves
Feeding		Greater energy gain in: Pumping Trapping Transporting particles to mouth Digestion
Coping with environmental factors		Greater morphological and physiological variability
		Greater eurytopy
		Tolerate higher rates of sedimentation
		Tolerate greater turbulence where sediments unconsolidated
	Generally tolerate greater turbidity	(Some species secondarily adapted for
	Probably require less food	high turbidity)
	??Susceptibility to predation??	
Larvae		Long planktonic stage
		?Spat possibly more resistant to predation

unimportant in modern communities of this type (e.g. Johnson 1964), and within subsets of marine invertebrates (particularly bivalves) in such communities (e.g. Stanley 1974a). This assessment of competition amongst bivalves as unimportant is particularly relevant to the present study, for by similar reasoning it can be argued that interspecific competition must be unimportant amongst co-existing brachiopods, and between co-occurring species of animals that are as similar as articulate brachiopods and filter-feeding bivalves. Also, by extrapolation one might contend that competition was unimportant in level-bottom communities and amongst articulate brachiopods and filter-feeding bivalves at all times in the past. Before trying to assess whether competition between these bivalves and articulates, and between these two groups of animals and other associated invertebrates, has been an important factor in the evolution of marine level-bottom communities, one should be aware of the cases for and against competition on the level bottom today.

'Competition' is used here in the sense of MacArthur (1972, p. 21): i.e. 'two species are competing if an increase in either one harms the other . . . provided the effect is reciprocal'. Therefore, to obtain proof of competition one has to follow changes in numbers of individuals of co-existing species, and to show that these changes are the result of an injurious effect of one species on another, a procedure that is particularly difficult on the level bottom where many animals live infaunally. Nevertheless, there is a small amount of direct and indirect evidence of competition, both in level-bottom communities in general, and amongst filter-feeding bivalves of such communities in particular.

Empirical evidence of competition

Competition in Recent level-bottom communities. Changes in fauna and often in bottom sediment accompanied the disappearance of eel grass along the Atlantic coast of North America in the 1930s. Johnson (1964) concluded, on the basis of evidence from

localities where the substrate had altered, that except for the disappearance of those few species that lived directly upon or amongst the eel grass, most faunal changes resulted indirectly from changes in bottom deposits. On the basis of this study, he argued that benthic communities are associations of largely independent species; this conclusion appears to be widely accepted by palaeontologists. However, Stauffer (1937) documented changes in a muddy lagoon on the Massachusetts coast, where on a first approximation no gross change in sediment appears to have occurred. He found that about 40% of the original fifty-four common species were no longer present at this locality after the loss of eel grass (Table 3). In addition, changes appear to have occurred in the relative abundances of some species that did not disappear. Although Stauffer's study was not sufficiently detailed to show such changes except where they were markedly pronounced, it is evident that at least two of the four burrowing species that were most common following the disappearance of eel grass had considerably increased their original numbers. This change in relative abundances appears to have greatly altered the dominances of the infauna, and therefore changed the character of the community. A plausible explanation for these results is that prior to the disappearance of eel grass, competitive interactions restricted the spread of certain species, but that these species subsequently expanded into the vacancies left either by the eel grass or by stronger animal competitors that had disappeared or decreased in numbers with disappearance of the eel grass. Therefore, Stauffer's study invalidates Johnson's conclusions, and appears to supply direct (albeit skimpy) evidence of the importance of competition within a marine level-bottom community.

The importance of competition can also be inferred indirectly from certain community structures. It is generally accepted that with time, community diversity increases by invasion of species from outside; and that where resources are limited, competition between successive invaders and established species forces all species to become increasingly more specialized (e.g. Hutchinson 1959). The result is a community in which the resources are partitioned amongst the different species. Therefore niche partitioning in a community is indirect evidence that competition has shaped the community. There are studies that show this type of resource sharing in level-bottom communities, both in the Temperate Zone (Sanders 1960) and in the Boreal Zone (Turpaeva 1948, 1949, 1953, 1954, 1957).

Sanders (1960) examined the *Nepthys incisa–Nucula proxima* community from soft-bottom sediments at 19 m depths in Buzzards Bay, Massachusetts, and found that only a few species out of a total of seventy-nine constantly dominate the community when either numbers of specimens or biomass are considered. In order to establish how

TABLE 3. Common species of eel grass community before and after destruction of eel grass.

Habitats occupied by species	Number of species	
	Before	After
Live on eel grass	7	1
Swim among eel grass	6	3
Live on mud surface	16	12
Burrow into mud	25	20

resources are utilized by the nine most abundant species (93% by number), he determined the spatial distribution of each, and from their methods of feeding and gut contents he determined the material that is ingested and from where on the bottom it is obtained. He found that each species utilizes a different range of the available resources. The same result is obtained for the eight most abundant species by biomass.

Turpaeva (1948, 1949, 1953, 1954, 1957) examined the feeding relationships amongst the dominant benthic invertebrates from four distinct regions in the Barents Sea. The animals were collected from depths of up to 300 m during five expeditions. The methods of feeding of all species were determined. In order to establish where the animals collected their food, composition of gut contents was analysed for each species and was compared with the substrate where the species lived. This information was supported or augmented by data from a large number of published papers on gut contents and/or the anatomy and physiology of feeding and digestion in the same or closely related species. On the basis of these studies Turpaeva recognized four feeding zones and five feeding groups for benthic invertebrates: within the bottom sediment (swallowers), on the surface of the bottom (collectors), the extreme bottom layer of water (filterers A), and higher bottom layer of water (filterers B, and waiters, i.e. animals that do not create their own currents). She noted that in general each of the more abundant species by biomass in a community feeds in a different trophic zone, and that where more than one species feeds in a single zone the biomass of the dominant species there greatly exceeds the biomass of all the other species. In the exceptional cases where two species in a single feeding zone have subequal biomasses, Turpaeva noted that either food or space is partitioned between them. She reported that other Soviet biologists working in the Barents Sea, White Sea, Sea of Azov, and Caspian Sea have found these same feeding relationships amongst the benthic invertebrates.

I have heard it argued that since food is usually abundant, Turpaeva's feeding zones have little ecological significance. Nevertheless, partitioning of the feeding space appears to be a reality in the Boreal communities; and as Turpaeva (1948) noted, food is strongly cyclical in these far northern waters. I have also heard it argued that Turpaeva's A and B filtering groups are ecologically unimportant since suspension-feeders actively create their own currents and may therefore obtain particles from different water levels. However, data of Reid and Reid (1969) show that sympatric suspension-feeding species of *Macoma* have predominantly different kinds of diatoms in their guts depending on whether their siphons project just above the bottom or a little higher into the water column.

Competition among Recent filter-feeding bivalves. Bradley and Cook (1959) noted that *Mya arenaria* usually lives abundantly in muddy areas, and *Gemma gemma* where it is sandy. However, when the two species co-exist, they found that an average of 25% fewer specimens of the small species of *Gemma* occur near the relatively larger *Mya* in the direction of current flow, than in other directions. They concluded that *Mya* has a deleterious effect on *Gemma*.

Eight species of *Macoma* may occur sympatrically along the coast of British Columbia. Reid and Reid (1969) attempted to determine niche overlap amongst the species by establishing for each species: orientation and activity of the siphon during

feeding, acceptance and transport of different kinds of particles to the mouth, and gut contents at the time of collection. They found the animals to consist of three deposit-feeders, four suspension-feeders, and one species that could feed in either way. Of the three deposit-feeders it appears that *M. secta* lives primarily on bacteria that coat ingested sand grains; gut contents of both *M. calcarea* and *M. lipara* consist mainly of small diatoms and flagellates, but *M. calcarea* can accept finer particles. Each of the suspension-feeders extends its siphon to a different maximum height; those that feed closest to the bottom (*M. elimata* at 1·5 cm, *M. incongrua* at 2 cm) have a large percentage of diatom chains in their guts, in contrast to those that feed higher in the water (*M. inquinata* at 2·5 cm, and *M. nasuta* at nearly 3 cm), which have mainly large solitary diatoms; in addition *M. nasuta* can accept and transport larger particles than can *M. inquinata*. Although further work is needed on the problem, the available information suggests that there is notable niche partitioning among the different species of *Macoma*.

Theoretical considerations on competition

Competition in level-bottom communities. A contradiction appears to exist between direct and indirect evidence on competition in Recent marine communities. On the one hand, controlled studies usually fail to demonstrate that competition actively occurs amongst animals in these communities (evidence summarized by Connell 1975); on the other hand, niche partitioning with respect to both food and space, which is indirect evidence of competition, appears to occur commonly (cf. Turpaeva 1948, 1949, 1953, 1954, 1957; Sanders 1960; Reid and Reid 1969).

Several authors have shown that intense predation in Recent invertebrate communities prevents competition (e.g. Paine 1966, 1971, 1974; Connell 1975; Menge and Sutherland 1976). Connell (1975) reviewed published evidence from controlled experiments illustrating that grazers and predators on the middle and lower levels of rocky shores in temperate zones usually eliminate their prey before these mature, with the result that these intertidal communities are normally undersaturated, and competition does not occur; and that harsh physical conditions in the upper part of the intertidal zone frequently kill young and small individuals so that likewise, competition is usually prevented. Nevertheless, he also showed that despite this predation, large numbers of prey in certain widely spaced year-classes survive to maturity and then persist for many years. As an explanation, Connell proposed that occasionally (i.e. every few years) natural enemies are reduced or harsh physical conditions are temporarily ameliorated so that the young of the dominant species survive to a stage that is invulnerable either to predation or to the severe physical conditions; and he reasoned that once the prey reaches this invulnerable size it competitively suppresses, displaces, or excludes other colonists. Therefore, from evidence and arguments presented by Connell, it appears that although competition can be seen to occur only rarely in rocky-shore communities, its effects are long-lasting, and it is very important in shaping the long-term structures of these communities.

Connell (1975) also argued that predation seems to be more intense where physical conditions are less severe (see also Jackson 1972), and that as a result, competition should occur in moderate environments even less frequently than on the rocky shore. Certainly, there is more direct evidence for competition in intertidal and reefal

environments than on the level bottom; but this evidence may be a function of the greater comparative difficulty in studying the ecology of level-bottom communities. Nevertheless, the argument that predation is more intense subtidally than intertidally is not the only factor to be considered in attempting to assess the prevalence of competition in level-bottom communities. For instance, many more species of invertebrates in general, not just of predators, inhabit the level bottom compared with the rocky shore, and all of these species (including epifauna, infauna, deposit-feeders, suspension-feeders, etc.) must be kept low in order for competition, either for food or space, to be prevented. Furthermore, as predation reduces existing prey there may be room for other species to move into the community (MacArthur 1972, p. 32). Interestingly, Woodin (1974) argued that the competitive interactions she studied amongst polychaetes in an intertidal mud flat should be more important subtidally, where the same animals also occur, but where disturbances by physical factors are considerably reduced. At present almost nothing is known about the complex biological interactions or the relative abundance of resources and general degree of saturation in level-bottom communities. Therefore, we do not know how often competition occurs in marine level-bottom communities, although we can argue on the basis of niche partitioning that it occurs sufficiently frequently to play a significant structural role, and presumably a significant evolutionary role. In order to study directly the effects of intermittent competition, it is necessary to monitor communities for extensive periods of time; the conclusion that competition is unimportant is drawn usually from studies that were conducted for only a couple of years.

Competition among filter-feeding bivalves. On the basis of considerable indirect evidence Stanley (1974a) argued that competition among subsets of suspension-feeding bivalves in marine level-bottom communities is generally weak and therefore relatively unimportant, and notably less important than that among mammals. Van Valen (1976) discussed extensively and disputed each of Stanley's arguments, primarily from the point of view of the theory of trophic energy in evolution. Van Valen showed that bivalves compete as much as mammals, but that competition in bivalves is low pressure, giving the appearance of no interaction at all; and he noted that the sum of many weak interactions can equal the sum of a few strong ones. Therefore, one cannot conclude by extrapolation from the Recent into the past that competition has been unimportant in the evolution of filter-feeding bivalves or (by further extrapolation) in the change in dominance from articulate brachiopods to filter-feeding bivalves in marine level-bottom communities.

Competition on the geological time-scale

Although intense competition may occur only rarely (on the human time-scale) in marine level-bottom communities, it appears to occur sufficiently frequently to strongly influence community structures. Therefore, it can be argued that competition affects changes in these structures, and that its cumulative effects over geological time are very important in community evolution.

Another point to consider in evaluating the importance of competition in the past is that ecological conditions have fluctuated greatly during the Phanerozoic, and have not always been the same as they are today. With every drop in sea-level, available

space on the shelf was reduced, resulting in smaller ecological niches and increased species packing (Schopf 1974; Simberloff 1974), or in fewer species at the same level of packing. Also, it has been argued on the basis of micropalaeontological evidence that there have been great shortages of food in the past, particularly during periods of massive extinctions (Tappan 1971; Tappan and Loeblich 1973). Therefore, one would expect competition to have been considerably intensified, and its effects to have been greatly enhanced, at certain times during the Phanerozoic. Furthermore, if predation has increased in intensity since the Palaeozoic (Stanley 1974b), competition may be less important in general in shaping communities today than it was in the past.

The above discussion indicates how risky it may be to extrapolate into geological time on the basis of what is observed in the present. Although some action may appear to be insignificant when viewed at any particular instant, its cumulative effects over geological time may be very important. Also, although natural laws remain the same, conditions under which these laws operate may change so greatly that different times in the past may bear little resemblance to the present.

RELATIVE ABUNDANCES OF ARTICULATE BRACHIOPODS AND FILTER-FEEDING BIVALVES THROUGH THE PHANEROZOIC

Brachiopods were the dominant suspension-feeding animals before the Middle Ordovician, when filter-feeding bivalves suddenly became important components of near-shore faunas. Although filter-feeding bivalves at this time moved into certain shallow-water environments that had been previously unexploited by articulate brachiopods (unpublished data from the Ottawa Valley) they also formed large diverse populations with these brachiopods, particularly in shallow subtidal habitats. Filter-feeding bivalves continued to evolve at a steady rate and continually invaded new adaptive zones (Stanley 1972). However, they failed to become established in deeper water, and articulates continued to dominate the offshore environments (Bretsky 1969a). These relative abundances were retained in marine benthic communities until close to the end of the Palaeozoic (Bretsky 1969a).

As late as the early part of the Upper Permian, off-shore faunas were still typically dominated by articulate brachiopods (Grant and Cooper 1973; Pattison et al. 1973), and local near-shore areas were dominated by filter-feeding bivalves (Pattison et al. 1973) or molluscs in general (Grant and Cooper 1973). The extensive marine regression that occurred near the end of the Permian resulted in considerable reduction or even elimination of the epicontinental seas, and a world-wide emergence of land (see papers in Logan and Hills 1973). During the early stages of retreat in the Upper Permian the relative abundance of molluscs, and of brachiopods that inhabited more shallow environments, increased (Grant and Cooper 1973). In fact even prior to this time the highly specialized articulates of the West Texas reefs were slowly being replaced by more broadly adapted pedunculate forms (Grant 1971). As regression continued the variety and numbers of articulates decreased and the abundance of filter-feeding bivalves increased (Dagis and Ustritsky 1973; Grant and Cooper 1973; Nakazawa and Runnegar 1973; Pattison et al. 1973); this increase in bivalve abundance was in some cases accompanied by a similar increase in gastropods (Nakazawa and Runnegar 1973) or ammonites (Grant and Cooper 1973). As bivalves increased in abundance,

their diversity increased in some places (Kanmera and Nakazawa 1973) and decreased in others (Pattison *et al.* 1973). Many families of articulate brachiopods became extinct in the later Permian (Waterhouse and Bonham-Carter 1976), and many of those that survived into the Triassic did so with only one genus (Dagis and Ustritsky 1973). Certain Palaeozoic families of filter-feeding bivalves slowly disappeared during the Upper Permian (Nakazawa and Runnegar 1973), and this disappearance was accompanied by a correspondingly slow appearance of the ancestors of Mesozoic bivalves (Stanley 1972; Kanmera and Nakazawa 1973; Nakazawa and Runnegar 1973). Of particular importance at this time was the expansion of the rapidly burrowing anomalodesmatids and trigoniaceans (Stanley 1972). The turnover of bivalve families at the Permian–Triassic boundary was very low, and except for the Pterioida and Veneroida, widely spread orders of filter-feeding bivalves suffered essentially no decline in their number of genera (Nakazawa and Runnegar 1973).

Ammonites and to a lesser extent bivalves (many of them pseudoplanktonic filter-feeders) are the only invertebrates that are known to have occurred in any abundance in early Triassic seas; lingulids are usually the only brachiopods recorded and they are comparatively much less abundant than the ammonites and bivalves (Kummel 1973*a*, *b*; Newell 1973; Rudwick 1970, p. 182). Since the lowermost Triassic has a complete spectrum of facies except for reefs, the absence of many invertebrate groups cannot be due to a lack of suitable substrate (Kummel 1973*a*, *b*). Articulate brachiopods began to increase in diversity and numbers in the Middle Triassic (Dagis and Ustritsky 1973), but never regained their former dominance (Rudwick 1970, p. 183). Typical Mesozoic genera of filter-feeding bivalves started to appear in the early Triassic and became common and widely spread by the late Triassic (Nakazawa and Runnegar 1973).

Articulate brachiopods were decimated again by extinctions at the Triassic–Jurassic boundary (Ager 1971), and by the Middle Jurassic the Atrypida, Spiriferida, and two of the remaining three aberrant Strophomenida groups had become extinct, so that the Terebratulida and Rhynchonellida were almost the only remaining articulates (Rudwick 1970, p. 173). From the Jurassic onwards filter-feeding bivalves dominated most macro-invertebrate assemblages in both numbers and diversity (Kauffman 1973). In fact brachiopods were insignificant in North American Jurassic (Hallam 1975, p. 131) and Cretaceous (Reeside 1957) faunas. In the Jurassic of Europe, dense low-diversity faunas, mainly of filter-feeding bivalves, dominated the littoral and very shallow subtidal or lagoonal environments, essentially in the absence of brachiopods (Ager 1965; Hallam 1975, pp. 75, 92; 1976). Although articulates were frequently a significant component of shallow, normal marine environments in the European Jurassic, Hallam (1975, pp. 46, 72, 73; 1976) considered that they were in general not nearly as important as filter-feeding bivalves. However, Ager has found (*in litt.* 1977) that throughout the Mesozoic, articulate brachiopods were dominant on rapidly lithified shallow-water carbonate sea floors, while burrowing suspension-feeding bivalves prospered on soft bottoms. These soft, shallow-water sediments of Mesozoic age also supported the occasional oyster (Ager 1965, 1976). Hallam (1976) reported that shallow marine basins that were poorly oxygenated in the Jurassic of Europe in some cases supported a fauna consisting mainly of deposit-feeding nuculoids, while basins with a higher oxygen content contained a more varied fauna in which brachiopods were subordinate to the relatively more important filter-feeding bivalves.

Ager (1965) noted that brachiopods were essentially absent from Mesozoic coral reefs but that they often thrived in association with these reefs; he noted that the best development of both Jurassic and Cretaceous brachiopods was in detrital fore-reef sediments, in contrast to their absence in back-reef lagoonal sediments in the Mesozoic in general. On the other hand, a diverse and often abundant fauna of filter-feeding bivalves occurred in Jurassic reefs (Hallam 1976). Deep-water environments generally lacked benthic invertebrates that left a fossil record, except for the deposit-feeding forms that left trace fossils (Hallam 1971, 1975, p. 97), and for the articulate *Pygope* which lived during the late Jurassic and early Cretaceous in fine-grained sediments where food was probably scarce (Ager 1965, 1967*b*).

Extinctions at the end of the Mesozoic only affected articulate brachiopods at the generic level, so that the character of the group has changed little since the middle of the Jurassic (Rudwick 1970, p. 173). However, since the end of the Mesozoic, articulates have again decreased in importance, and in shallow-water environments have been largely replaced by bivalves (Ager 1967*a*). This articulate decline coincided with a marked Cenozoic decrease in rapidly lithified carbonates, and articulate brachiopods are found in the Tertiary of Europe where there are limestones (Ager *in litt.* 1977). Today articulates are a very insignificant part of the marine fauna (Ager 1967*a*).

An idealized summary of the relative dominances of the two groups is given in text-fig. 1.

SHARING THE NEAR-SHORE REGION DURING THE PALAEOZOIC

Although filter-feeding bivalves and articulate brachiopods have overlapped considerably in utilization of resources, the two groups continued to share the near-shore region from the Middle Ordovician until close to the end of the Permian without the physiologically superior bivalves ousting the brachiopods. An explanation is that although the overlap is considerable when the whole of the Phanerozoic is considered, partitioning generally occurred between these animals in the Palaeozoic. Professor Ager wrote (*in litt.* 1977) that in his experience brachiopods and bivalves rarely occurred together in abundance either in the Palaeozoic or in the Mesozoic. Since brachiopods are basically considerably more tolerant of high turbidity than are filter-feeding bivalves, shallow soft muddy bottoms were usually inhabited by free-living articulates in the absence of filter-feeding bivalves (Steele-Petrović 1975). In less turbid Palaeozoic environments where both groups co-existed, although apparently rarely, articulates typically lived epifaunally and attached by the pedicle, in most cases probably to firm surfaces such as hard substrates, or on muddier bottoms to exposed shells and other fragments (discussed above). In contrast, Palaeozoic filter-feeding bivalves were endobyssate, epibyssate, free-burrowing, or free-living epifaunal forms (Stanley 1972), and therefore in most cases must have inhabited slightly different micro-habitats from the articulates. Division of food amongst the different sympatric species might have occurred (e.g. Walker 1972), but supporting evidence is scarce. Nevertheless, partitioning of space must have contributed to the ability of the two groups of animals to share the near-shore region for so long a time.
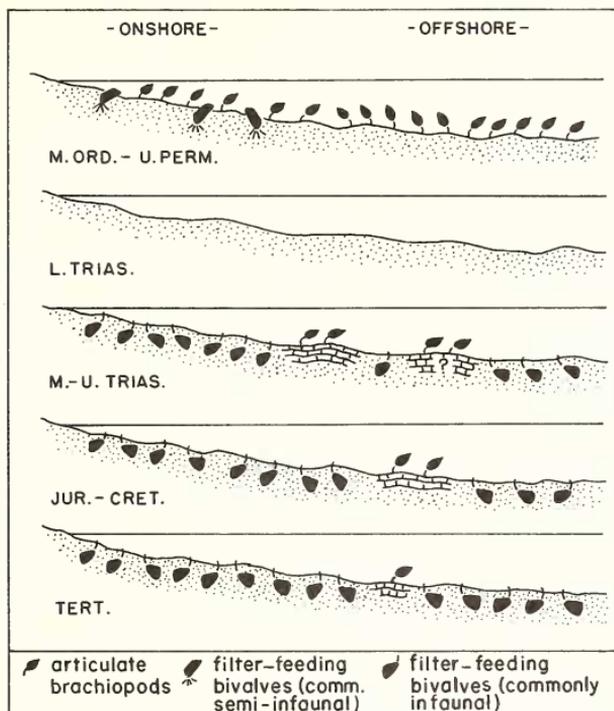
TEXT-FIG. I. Idealized diagram of dominances of articulate brachiopods and filter-feeding bivalves in level-bottom communities.

THE RESTRICTION OF FILTER-FEEDING BIVALVES TO NEAR-SHORE COMMUNITIES UNTIL THE LATTER PART OF THE PERMIAN

Stanley (1972) suggested, but no longer believes (Stanley *in litt.* 1976), that because of the stenotopic nature of established off-shore articulates, filter-feeding bivalves were confined to near-shore regions in the Palaeozoic. If that had been the case these bivalves would probably have been restricted to the intertidal zone rather than also occurring abundantly in shallow, normal marine environments. Another explanation is that deeper environments of the Palaeozoic inland seas were generally inhospitable for filter-feeding bivalves, or at least more favourable for articulates than for these bivalves. As mentioned above, brachiopods would probably have had an advantage over primitive filter-feeding bivalves where turbidity was high. However, since off-shore sediments during the Palaeozoic appear to have ranged from sand to mud (Bretsky 1969*a*), turbid conditions could not have been the only factor that kept filter-feeding bivalves close to shore. One can also discount the possibility that these bivalves

were physiologically unable to live in deeper water, for bivalves (such as the Ordovician genus *Lyrodesma*, in Bretsky 1969*b*) appeared off-shore at various times during the Phanerozoic, although they failed to spread and become important numerically. There is also the consideration that brachiopods compared with filter-feeding bivalves can probably live where food is less plentiful (discussed above). However, benthic fauna was abundant during most of the Palaeozoic, suggesting that scarcity of food was not a problem then.

A more satisfactory explanation can be found in the Stability-Time hypothesis of Sanders (1968). Ecologists generally agree that an outside species can invade an undersaturated community more easily than it can a community at carrying capacity. Hutchinson (1959) argued that invasion probably only succeeds where one or more species are fluctuating and are under-represented at a given time. Since near-shore communities are in a region of high environmental stress and are subject to continual disturbance, their diversity generally remains low (Sanders 1968, 1969; Slobodkin and Sanders 1969), and their species are subject to large fluctuations. Shallow subtidal environments must also be subject to frequent (geologically speaking) unpredictable physical disturbances that are severe enough to disrupt community equilibria and produce faunal fluctuations. Therefore, once bivalves become successful marine benthic invertebrates, possibly due to an adaptive breakthrough of the byssus as a post-larval organ in the Ordovician (Stanley 1972, 1975), they were able to invade successfully and to become prominent in fluctuating intertidal and shallow subtidal communities. In contrast, physical disturbances, unless very severe, are considerably dampened in deeper environments. As a result of long-term predictability, off-shore communities evolve relatively high diversities (Sanders 1968; Dayton and Hessler 1972), which the Stability-Time hypothesis attributes to increased niche specialization (Sanders 1968, 1969). Resulting community equilibrium in these environments is probably rarely disturbed more than slightly by physical forces, and community structures should be maintained for considerable periods of geological time.

Several authors (Dayton and Hessler 1972; Menge and Sutherland 1976) have argued that high diversity in the deep sea today is explained better by predation than by increased niche specialization as suggested by Sanders. The predation theory proposes that prey populations are maintained at sufficiently low densities so that resources are rarely limiting, thus permitting great overlaps in resource utilization (Dayton and Hessler 1972). Although this theory may explain Recent deep-sea diversity (but see Grassle and Sanders 1973), it does not seem to be an appropriate explanation for conditions that were present in marine level-bottom communities during the Palaeozoic; it can be argued that if off-shore Palaeozoic communities had been undersaturated as predicted by the predation theory, filter-feeding bivalves almost certainly would have invaded. In contrast, increased niche partitioning which gives rise to saturated communities adequately explains the restriction of these bivalves close to shore.

A single species of filter-feeding bivalve attempting to invade an off-shore community in the Palaeozoic undoubtedly had essential requirements in common both with a number of established species of articulate brachiopods and with other less similar animals such as bryozoans, crinoids, annelids, and soft-bodied organisms that have not been preserved. Although an attempted filter-feeding bivalve invader must

have faced competition from several different kinds of established animals, competition was probably greatest from articulates because of their dominance and their greater ecological overlap with these bivalves. Nevertheless, since the needs and living processes of animals inhabiting a diverse community are highly inter-related, fluctuations not only in articulate brachiopods but in a large number of diverse established species, amounting to disruption of the community structure, might have been necessary before filter-feeding bivalves were able to invade these ancient communities. The palaeontological evidence appears to support this suggestion, for it was not until after the Permo-Triassic crisis, when articulate brachiopods and many other groups were decimated, that filter-feeding bivalves became established off-shore.

Although faunal changes occurred in off-shore communities throughout the Palaeozoic, these changes, as recorded in the fossil record, amounted primarily to replacement of one articulate brachiopod by another, and articulates continuously dominated the off-shore scene (Bretsky 1969a). As mentioned above, brachiopods as a group have a relatively low potential for morphological and physiological versatility, and orders of articulates have differed mainly in shape of the shell and configuration of the lophophore; they are also ecologically conservative, and have always been epifaunal suspension-feeders and generally pedically attached, although free-living forms were common during the Palaeozoic. Therefore, undersaturation, or local extinction of a single articulate species might lead to its replacement in almost exactly the same niche, by another, possibly phylogenetically distant, articulate. Such fluctuations in brachiopods could possibly result from slight environmental changes, which must have affected even off-shore communities many times during the Palaeozoic.

Even when major changes occurred off-shore in the articulate faunas at the end of the Devonian, filter-feeding bivalves did not move into this region; this fact implies that community structures were not intensely disrupted at that time, and that much of the faunal change was the result of substitution of one species for another, rather than wholesale extinctions and subsequent colonization of open habitats. On the basis of this reasoning, it can be argued that off-shore communities, at least as indicated in the fossil record, retained essentially the same ecological structures throughout the Palaeozoic.

The above arguments may have general implications, particularly for the Palaeozoic; i.e. new higher taxa of marine invertebrates which differed significantly from pre-existing forms, and which became ecologically successful during periods of relative geological stability when off-shore communities were well established, may in general have achieved initial prominence in shallow environments where physical disturbances are more intense; these new taxa, even if they could physiologically tolerate off-shore conditions, may have been restricted to shallow waters until a time when community structures off-shore were disrupted. However, there is evidence to suggest that predation has increased in intensity since the Palaeozoic (Stanley 1974b) possibly causing a decrease in the density of prey populations off-shore (Dayton and Hessler 1972), and hence increasing the ease with which invasions may occur. Therefore, the above implications may not apply in most post-Palaeozoic situations.

INCREASE IN IMPORTANCE OF FILTER-FEEDING BIVALVES AND DECLINE OF ARTICULATE BRACHIOPODS

Stanley (1974b) attributed the decline of articulate brachiopods and the change in dominance of articulates and filter-feeding bivalves to the inability of articulates to cope with advanced Mesozoic predators, namely teleost fishes, crabs, and drilling gastropods. However, the first appearances of fossilized members of these groups occur after the Permo–Triassic and Triassic–Jurassic declines in brachiopod dominance; teleost fishes first appear in the Upper Jurassic (Andrews et al. 1967), drilling gastropods in the Upper Cretaceous (Sohl 1969), and crabs in level-bottom communities in the Cretaceous (Glaessner 1969). Therefore, one cannot convincingly argue that predation by these animals caused either the extinctions or lack of re-expansions of articulates at the Permian–Triassic and Triassic–Jurassic boundaries; it could have been a factor only in the final decline of articulate brachiopods at the end of the Mesozoic and during the Cenozoic. In addition, both articulates and filter-feeding bivalves probably were subject to considerable predation during the Palaeozoic, particularly from starfish and possibly also from nautiloids. There is fossil evidence to show that predatory starfish have been present at least from the Upper Ordovician, and that they have used the very effective method of external digestion at least from the Middle Devonian (Spencer and Wright 1966). Although filter-feeding bivalves may have been better protected from these predators than were articulates (Stanley 1974b), large changes in the relative dominances of the two groups of animals did not occur between the Middle Ordovician and about the end of the Palaeozoic, thus giving no evidence that efficient Palaeozoic predators reduced the abundance ratio of articulates to filter-feeding bivalves. In fact, MacArthur (1972, p. 94) argued that, except on an island, predators other than man are usually incapable of causing complete extinctions.

The known relative abundances of articulate brachiopods and filter-feeding bivalves in Mesozoic level-bottom communities can be explained in terms of physiological differences between the two groups of animals as follows. There is evidence from the fossil record to suggest that the Permo–Triassic extinctions were caused or contributed to greatly by: (1) intolerable physical conditions which resulted as the sea withdrew (see papers in Logan and Hills 1973); (2) decrease in shelf area due to regressing seas (Schopf 1974; Simberloff 1974); (3) low productivity of primary producers (Tappan and Loeblich 1973). As the sea retreated, many species disappeared. Those that disappeared first and suffered most were highly specialized and/or stenotopic forms (cf. previous section and section on relative advantages), which strongly suggests that changing physical conditions contributed significantly to many extinctions. The effect played by competition, either for food or space, is more difficult to assess. As shelf area decreased and food became scarce competition may have ensued, unless intolerable physical conditions had resulted in extinctions that more than compensated for the decreased availability of the necessary resources. Eventual extinction of many species may have been accelerated by predation and/or competition once populations dropped below a critical value (MacArthur 1972, pp. 92–97). Therefore, it can be argued that filter-feeding bivalves suffered relatively fewer extinctions at the end of the Palaeozoic than did the articulates because of the greater eurytopy of these bivalves and possibly

also to some extent because of greater competitive ability. The Triassic–Jurassic extinctions also affected articulates considerably more than filter-feeding bivalves, possibly for the same reasons, as suggested by the fact that I could find no evidence for biased loss of habitats that were particularly favourable for articulates; however, these possible causes for Triassic–Jurassic extinctions cannot be tested at present.

The dearth of benthic faunas in the Lower Triassic contrasts with the more common occurrence of nektonic forms (see above), and suggests that bottom living conditions were highly unfavourable at that time. By the Middle Triassic these conditions had begun to improve, as indicated by a more diverse and abundant benthos. It can be argued, on the basis of comparative physiology of articulates and filter-feeding bivalves, that once benthic conditions started to improve, these bivalves should have had a colonizing advantage over the articulates for the following reasons: (1) because of the greater eurytopy of filter-feeding bivalves, physical conditions that were tolerable for them would have been widespread before suitable conditions for the more stenotopic articulates had developed, and filter-feeding bivalves generally should have emerged from the environments where they sought refuge during the Lower Triassic before articulate brachiopods did; (2) since bivalve larvae generally have a planktonic stage of several weeks, in contrast to a very short or absent planktonic stage of articulates, filter-feeding bivalves should have spread into unoccupied areas relatively more quickly; (3) since these bivalves can effectively cope with a range of environmental conditions they should have become widespread in a variety of open habitats; (4) if food were in short supply, the bivalves, because of their more effective feeding methods, usually should have been favoured.

This ability of filter-feeding bivalves to extensively colonize level-bottom environments ahead of articulate brachiopods in the Middle Triassic, adequately explains the subsequent dominance of these bivalves over the articulates. In addition, after articulates declined in the Triassic–Jurassic extinctions, filter-feeding bivalves, which were relatively little affected, must have moved into many of the habitats that were previously occupied by the articulates, thus increasing the dominance. In agreement with modern ecological theory, one would expect that as environmental conditions ameliorated in the Middle Triassic, and invasions (not only of filter-feeding bivalves but also of other relatively eurytopic benthic invertebrates) increased, the pioneer level-bottom communities would have developed greater diversity and greater resistance to outside invasion. When conditions became favourable for most articulates and they attempted to spread, they probably encountered resistance of varying intensities from interacting species in different established communities. Many environments (e.g. shallow subtidal, shallow lagoonal, reefal) that were occupied by articulate brachiopods during the Palaeozoic, contained filter-feeding bivalves but no articulates in the Mesozoic (see above). There is no reason to suggest that Mesozoic articulates were unable to tolerate these environments. Rather, their exclusion can be explained by an early establishment of other invertebrates. An invading articulate species would probably have competed mainly with established filter-feeding bivalves, but also with other less similar animals that utilized some of the same resources. The success of an articulate attempting to invade a low-diversity community would probably have depended on the degree of overlap, particularly with the established bivalves. Its chances of success in a relatively diverse community consisting of highly

specialized and interacting species would probably have been low, particularly if some of the established species had been filter-feeding bivalves with considerable overlap in requirements with the invader. Because of a scarcity of information on Triassic communities, and on both succession in Mesozoic communities in general and life histories of the particular Mesozoic species involved, much of the present discussion is necessarily generalized. There are sufficient data to permit only those communities that inhabited soft muddy bottoms to be discussed in slightly greater detail.

As noted above, filter-feeding bivalves moved into and occupied soft muddy sediments during the Mesozoic; except for the occasional oyster, these bivalves were predominately infaunal siphonate forms. This situation contrasts greatly with that of the Palaeozoic, when soft muddy environments were inhabited by abundant free-living epifaunal articulates. Since siphonate bivalves are much better suited than are most other forms of filter-feeding bivalves for handling suspended sediment, and as a result for occupying soft muddy environments, and since eulamellibranch gills are imperative for deep burrowers, the presence of the siphon and almost certainly the eulamellibranch gill permitted filter-feeding bivalves, early in the Mesozoic, to move in abundance into these open muddy environments (cf. Stanley 1968, 1972). Also, certain oysters, both extant and fossil, are secondarily adapted physiologically for handling large quantities of mud (Nelson 1938). One cannot argue convincingly that unsuitable physical conditions prevented articulates from re-occupying these environments during the Mesozoic; after all, these animals had the potential to evolve numerous highly specialized morphologies which could effectively cope with soft muddy substrates, as illustrated in the Palaeozoic; also, although most Palaeozoic mud-dwelling articulates became extinct at the end of the Permian, there were a few Mesozoic articulates such as *Terebratulina* and related forms which were specially adapted for life on a muddy bottom (Ager *in litt.* 1977), and these genera must have had a potential to radiate. In contrast, the absence of Mesozoic articulates in muds can be explained adequately by the presence of filter-feeding bivalves. In general, when Mesozoic articulates suited for life on muddy substrates began to spread, as conditions became favourable for them, they probably encountered competition, particularly from oysters and siphonate bivalves, but also from other invertebrates that had previously become established in the mud; and any new mutant that could have exploited muddy bottoms would have faced similar competition. Although articulates and siphonate bivalves lived at different horizons, siphons of bivalves reached to the surface or a little above, and bivalves would have fed where articulates lived and fed. Since both groups utilized essentially the same food and feeding space, intense competition could have resulted. Therefore, it can be argued that the presence of early colonizers, and in particular filter-feeding bivalves, prevented the Mesozoic articulates from realizing their potential for life on soft muddy substrates. If filter-feeding bivalves had been unable to exploit muddy environments, Mesozoic articulates probably would have become re-established on these muds.

The ability of filter-feeding bivalves to colonize earlier and faster than articulates undoubtedly affected the character of radiations of the two groups. Bivalves had more opportunity to evolve new forms as they expanded into a greater number of different environments, and articulates remained relatively conservative, even for them, because they were unable to recolonize many of the environments that they had occupied

during the Palaeozoic. The fact that articulates were excluded from Mesozoic soft muds and reefs, two habitats in which they had been highly specialized in the Palaeozoic, probably contributed greatly to the Mesozoic–Cenozoic conservativism of the group.

This situation with articulate brachiopods, where they suffered several severe extinctions but failed to subsequently regain their previous importance, contrasts with that of ammonoids (Rudwick 1970, p. 183), which came close to extinction at the end of both the Permian and Triassic, but unlike brachiopods re-radiated significantly (Arkell 1957; Teichert 1967) and re-expanded in importance to again become a dominant part of the fauna. A plausible explanation for this difference is that no other animals had moved in to fill the roles held by the ammonites before these extinctions.

IMPLICATIONS FOR FURTHER RESEARCH

Changes in dominance of articulate brachiopods and filter-feeding bivalves in marine level-bottom communities are interpreted in this paper in terms of physiological differences between the two groups. Although the proposed explanations fit the available evidence, additional information is essential to verify the ideas presented here and to permit solving of numerous problems that cannot be answered at present. In particular, more field and/or laboratory data are needed on the biology of the two groups (particularly articulates) and on the structure of marine level-bottom communities through time. The collection of such data requires experts in several normally unrelated disciplines. I hope that this paper draws the attention of specialists in the relevant fields to the outstanding problems and to the importance of these problems for understanding the evolution of marine level-bottom communities.

SUMMARY AND CONCLUSIONS

1. During the Phanerozoic, articulate brachiopods and filter-feeding bivalves have overlapped considerably in habits and habitat requirements.

2. The food of brachiopods and filter-feeding bivalves is essentially the same.

3. Compared with brachiopods, filter-feeding bivalves gain more energy in pumping, trapping, transporting particles to the mouth, and digestion.

4. Filter-feeding bivalves generally cope better than articulate brachiopods with different environmental conditions.

5. At present there is insufficient information to determine relative susceptibility of articulates and filter-feeding bivalves to predation.

6. The relatively long planktonic stage of filter-feeding bivalve larvae permits quicker colonization and expansion than by articulate brachiopods.

7. The importance of competition cannot be dismissed either in Recent level-bottom communities, in general, or within subsets of marine invertebrates (especially bivalves) of such communities, in particular.

8. At certain times during the Phanerozoic, competition may have been considerably more intense than at present.

9. Between the Middle Ordovician and about the end of the Permian, articulate brachiopods and filter-feeding bivalves shared the near-shore environments, while

articulates dominated off-shore. After the Permo-Triassic extinctions, filter-feeding bivalves generally dominated over articulates. This dominance increased again at the Triassic–Jurassic boundary and again during the Cenozoic.

10. There is evidence that partitioning of space contributed to the co-existence of articulate brachiopods and filter-feeding bivalves close to shore during the Palaeozoic.

11. Physical disturbances close to shore permitted filter-feeding bivalves to become established in near-shore communities early in the Palaeozoic. The dampening of disturbances away from shore enabled off-shore communities to become highly diverse, and to maintain essentially the same ecological structures throughout the Palaeozoic. Filter-feeding bivalves could not fit into these established community structures, and it was not until these communities were disrupted at the end of the Permian that the bivalves moved off-shore.

12. The decline of articulate brachiopods and change in dominance of articulates and filter-feeding bivalves cannot be attributed to predation.

13. This decline and change in dominance can be attributed to physiological differences between the two groups of animals. Filter-feeding bivalves suffered less than articulates at each period of extinction. Following the extinctions, these bivalves were able to re-colonize a large variety of widely spread open habitats earlier and faster than the brachiopods. Competition then probably prevented articulates from invading many regions. With each wave of extinction, filter-feeding bivalves gained prominence at the expense of articulate brachiopods.

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